THE MECHANISM OF THE WATER TIGHT DOOR OF THE *UTRICULARIA* TRAP

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(WITH FIVE FIGURES AND ONE PLATE)

Introduction

Of the various devices found among plants with the function of entrapping animals, none has been more intriguing than that of *Utricularia*. Interesting and complex as are the pitchers of *Sarracenia, Darlingtonia, Nepenthes, Cephalotus,* these are passive in their behavior, aside from the secretion of digestive enzymes [HEPBURN and his co-workers (**10**)]. Far more remarkable are considered the submersed *Aldrovandia vesiculosa* L. and the land form *Dionaea muscipula,* the leaves of which, when stimulated, respond by closing over the unwary insect or other animal which touches the sensitive hairs (**3, 6**). *Utricularia,* however, possesses bladder-like traps which are purely mechanical in their action when once set, and entrap small animals in much the same way as does a mouse trap of the old-fashioned kind. The setting, which is automatic, is the result of a peculiar physiological behavior of the walls of the bladder (recently studied by CZAJA). Beyond this, the trapping action is mechanical, the captured animals being hopelessly ensconced within, when death and digestion finally overtake them. As will be seen, the setting of this trap results from negative pressure of water within. The maintenance of this reduced pressure is made possible by the tight closure of the door. Many attempts have been made to explain how this efficiency is attained and it was the unsatisfactory answers to the question which prompted the present inquiry.

The structure of the *Utricularia* trap (or bladder, as it is frequently called) is so well known and has been so often described, that repetition is unnecessary here (see **1**). There are numbers of species, which differ in various details, but they have in common the trap structure, and all appear to work in the same way (**8, 9, 11**). In the present paper attention is confined to *Utricularia minor.* In this species the trap is compressed pear-shaped, with the entrance at the narrow part where it is truncated. The entrance is guarded by a crescentic ridge, the threshold (plate II, fig. 1), against which rests the edge of the door. The hinge of the door is a semicircular fold attached to the walls of the trap from the inner edge of the threshold on one side where it gives on the wall of the bladder about the opening to the corresponding point on the other side. The structure of the door is such that, when its cells are alive and turgid, it has strong outward spring, but is kept from springing too far forward by its own shape and emplacement (fig. 1). If cut away from the sides of the trap, it springs so far forward that the entrance is entirely open. The capacity of the door for bending resides in the form of the component cells (plate II, fig. 7), which have been often described. There is a vestibule-like space in front of the door, from the inner surfaces of which extend glandular trichomes. Similar trichomes, but of more varied forms, grow out also from the outer surface of the door; and in addition to these there are (usually) four stiff, pointed trichomes which serve as levers, and may be appropriately called trigger hairs (fig. 1). These are attached obliquely to the outer surface of the door near the middle point of the lower free edge. The part of the door

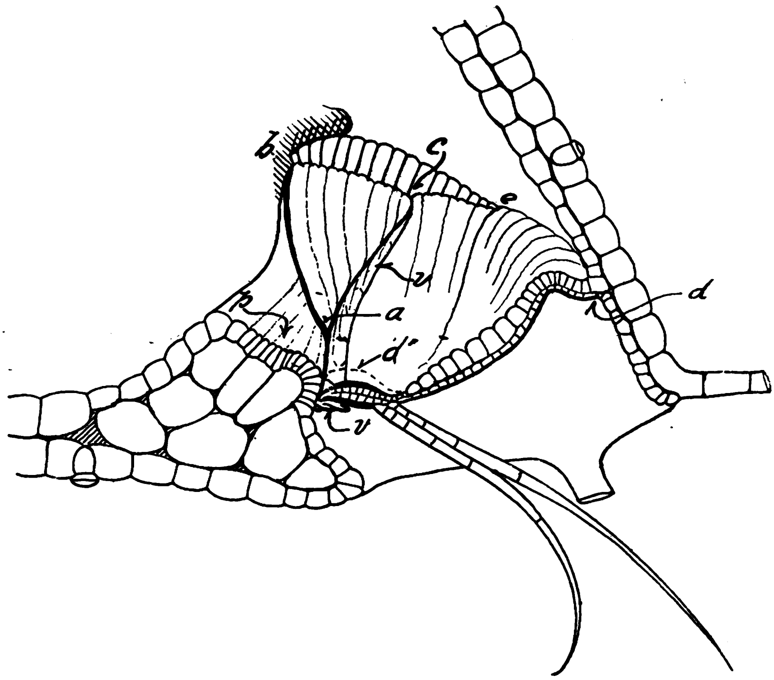

FIG. 1. Diagram of sagittal section and perspective view of the entrance of a trap with the door in the set position and showing the articulation of the door with the wall.

d e. Transverse reach.
b e. Lateral reach.
b c. Articulation with the threshold.
b a. Lateral reach of the free edge of the door, crossing the threshold.
a d'. Middle reach of the door lying in front of the threshold.
The dotted line below d', shows the tripping position of the door.
v. The veil or valve.
p. The pad.

between the insertion of the trigger hairs and the free edge is well thickened (fig. 1) and has a much thickened cuticle (**12**); the trigger hairs and the thickened door edge are so firmly of a piece that when the hairs are bent, the door edge bends with them. The fulcrum for this lever movement is furnished by a very thin spot in the door, just above the insertion of the trigger hairs. It must further be understood that the door is domed, the convex surface being directed outwardly. It is thus able to withstand a considerable, but unmeasured, pressure of water. This pressure results from the circumstance that the water within the bladder is pumped out by the walls, the lateral of which consequently become incurved, as it were collapsed, when the trap thus becomes set. It is to be especially remarked that the set condition is permanent (**12, 6, 13**), from which it must be concluded either that the door does not allow any leakage of water into the interior, or that the cells of the walls can pump it out as rapidly as it gets in.

The foregoing statement of the case is common knowledge and may be summarized briefly as presently follows.

(a) The normal, that is, undamaged or not otherwise discommoded trap, is, when set, water tight as respects mass movement of water (**12, 6**). For only a brief period (less than 1/16 sec.) can water enter. This occurs when the trap is sprung.

(b) The set condition results from the withdrawal of water from the interior of the bladder or trap, through the walls. There is thus set up a reduced pressure of water within. In this condition the lateral expanses of the wall of the trap are strongly inbent, so that they become markedly concave (**2, 12, 6, 13**).

(c) When in this condition, the concave sides of the trap can act as relatively powerful springs. By their sudden bulging out, they can pull through the entrance a considerable column of water with great suddenness. Any animal not too large, which happens to lie within this column of water, is immediately carried into the trap.

(d) The sudden bulging out can occur normally only if the trap is sprung (**12, 6**). This happens when the trigger hairs are suitably disturbed, namely, in such fashion that the middle portion of the free edge of the door is lifted. At the moment of lifting, the side walls spring out, the whole mechanism passing instantly from a state of labile into one of stable equilibrium.[1]

(e) The walls hereupon begin to pump out the water at such a rate that the trap may become set again after the lapse of 15 minutes (**12**) or usually

[1] Springing of the traps occurs when the plant is raised out of the water into the air and the water allowed to drain off. BROCHER noticed a clicking sound caused thereby. MERL's explanation that the surface tension of the films of water about the trigger hairs accomplishes the tripping is probably correct.

a rather longer period (**13**). We (LLOYD and R. D. GIBBS) have observed the capture of a second worm 35 minutes after the first capture. As soon as a sufficient volume of water has been pumped out, that is, when the sides of the trap have become more or less concave, the trap has become automatically reset.

(f) The pumping out of the water is a function of the walls, which CZAJA described as semipermeable. The action is referred to the two- and four-armed trichomes, which are regarded as absorbent structures (**12, 6**). There is insufficient proof of this, but the matter does not enter into the present discussion.

(g) As stated in (a) above, the set condition is permanent. MERL saw that no dyes enter even during a period of days. CZAJA showed, by passing a human hair underneath the edge of the door, that unless the opening at the entrance is completely closed, the trap does not reset itself.

(h) This hermetically sealed condition, to use MERL's phrase, is owing, according to all observers except BROCHER and WITHYCOMBE, to the firm pressure of the lower free edge of the door against the top of the threshold. According to the majority view the effective sealing of the entrance results from the pressure, eventually produced by the turgor of the door cells, of the free edge of the door against the opposed surface, but seconded by the presence of mucus (**13**) or mucilage which acts as a plugging material, filling the reentrant angle formed at the edge of the door. All students of the matter have agreed on this latter point. The various views with regard to the articulation of door edge with the threshold are indicated by the following passages: ". . . ihr freies Ende auf einem hufeisenförmigen Rahmen als Widerlager ruht" (**8,** 1889, p. 152); ". . . mit der freien vierten Seite dem den Antennen gegenüberliegenden dicken, mit ebenfalls Schleim bildenden Zellen besetzen Mündungsrande von unten d.h. vom Blaseninnern her, anliegend" (**4,** 1888, p. LIX); "ihre Klappe schliesst mittels eines Schleimwulstes so fest, dass aus dem Innern nichts heraustreten kann" (**11,** 1910, p. 211). "Die höchst elastische Klappe die . . . dem Widerlager ziemlich fest aufliegt . . ." (**12,** 1922, p. 73). "Der mittlere Teil liegt dem Polster auf und ist schmal, die seitlichen Teile liegen ebenfalls auf . . ." (**6,** 1922, p. 713); BROCHER, sensing the unsatisfactory character of these or similar descriptions, remarked "s'il était disposé aussi simplement que cela est representé généralement dans les livres, cet état de pression negativ ne pourrait exister, et se maintenir, à l'interieur de l'utricle. Mais tel n'est pas le cas. La disposition est un peu différente et rend cet état de chose possible." He then states that the inward flexing of the sides has the effect of augmenting the curvature of the door in such fashion that "le bord libre de celui-ci s'applique d'autant plus exactement contre le rebord (X in his figure) de l'utricle qui lui est opposé, que la courbure de l'opercule est plus considerable" (**2**, p. 43–44). "This margin (of the valve or door) is sharp, thin and smooth and rests on the edge of a rim or collar which projects into the interior of the bladder. The collar *obstructs any outward movement* (italics mine) with the result that the valve (door) can only open inwards" (ARBER, 1920, p. 93). The last quotation is given, not in criticism of its author, but because it summarizes the then accepted view.

WITHYCOMBE (**13**), however, became still more aware of the discrepancy between the accepted accounts and the behavior, and came to believe that the edge of the door rests, not on the top of the threshold, but in a "slight groove" in front of the "collar cells." His evidence, however, derived from fixed and paraffin-sectioned material, misled him on this point, the threshold tissues having shrunken so much as to completely distort the shape of the upper surface. As will be shown, the door edge rests against the top of the "collar cells," or pad, and not against their forwardly directed lateral faces. WITHYCOMBE did not apparently apprehend the fact that the door edge crosses the threshold (**6**). The sealing "mucus" he supposed to have been secreted by the middle layer of the "collar cells" (his figure 5, **13**). WITHYCOMBE, therefore, believed rightly that the door edge presses inwardly against an outwardly opposing surface, but failed to determine what surface, and further accepted mucilage or mucus as the sealing material.

Having thus been led to investigate the matter, it has been possible to show that the mechanism which prevents the inward leakage of water into

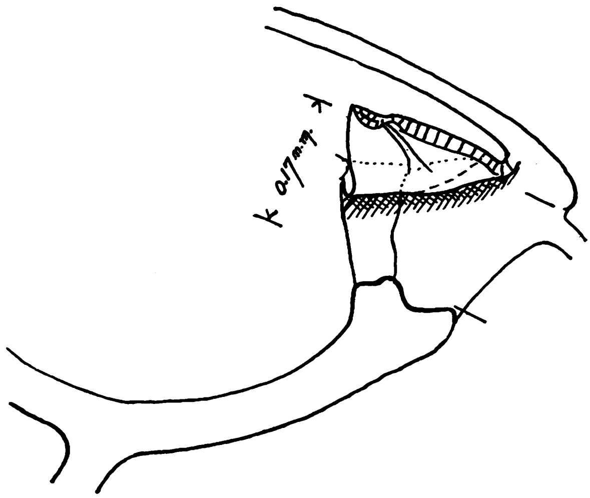

FIG. 2. Position of the door when widely opened.

the trap is not the door alone with a seal of mucilage, but the door acting in cooperation with a valvular membrane attached to the front margin of the threshold. Furthermore, the lower edge of the door lies, when in normal position, not on the threshold, nor pressing outwardly against the outer raised margin, but *pressing inwardly against the outer aspect of this margin.* It is this emplacement of the free edge of the door along a *ligne d'appui,* coupled with the valvular action of *a curtain-like membrane, that together prevent the seepage of water.* The permanence of the set condition of the trap, depending on the foregoing, has been verified by me, with the cooperation of Mr. R. D. GIBBS. In addition we have also determined the behavior of the traps, finding ourselves in agreement with CZAJA and MERL especially in regard to the springing of the trap. We have done this with a needle point and have watched animals (small worms) being entrapped,[2] and have come to the conclusion that the downward movement of the trigger hairs (that is, away from the plane of the antennae) is the most effective, if not the only normal condition for the release of the door. I find that unless the lower edge of the door is engaged by pressing inwardly against the raised outer margin of the threshold (figs. 1, 4), it is unable to resist the pressure of the outer water (assuming the trap to be set) and accordingly bends inwardly, admitting water, or air if water is not present, as BROCHER observed. To release the door edge from this engagement, it must be lifted free of the opposing margin of the threshold. The moment this is accomplished the door gives way entirely to the inrushing water. It is now in order to present an account of the mechanism as thus comprehended. The significance of a number of details of structure hitherto negligible, or at any rate neglected, will now come to light.

Observations

First we will take up the opening into the trap and the threshold. Considering, for the purpose of description, that the antennae are attached to the *upper* lip of the trap, the threshold bars the entrance a short distance within the vestibule. The plane in which it lies will be used as a plane of reference in the following description.

THE THRESHOLD

The threshold is a massive curved structure, the upper surface of which forms a flattened crescent with the horns projecting slightly toward the interior (figs. 1, 4; plate II, figs. 1, 2, 9). Looked at from above, the eye

[2] A motion picture has been made of this, using no artificial assistance, depending wholly on the behavior of the worm. This picture was exhibited at the New York meeting of the Botanical Society of America, December, 1928.

of the observer being in the threshold-plane, the forward or outward margin is curved like a conventional Cupid's bow, the chief curve, that of the body of the bow being in the middle, the rear or inner margin, straight or nearly so. The inner surface extends steeply downwards and is clothed with bifid glandular or absorbing hairs, whatever this may mean. There appears, however, to be another margin within this one just described. This is due to the presence of a pad or mat of epithelium composed of glandular trichomes (**13**) (trapezoidal as seen from above) which in a transverse section of the threshold appear columnar with rounded free surfaces. The shape of the pad is such that the rear limb is symmetrical with the forward limb, being broad near the horns and in the middle (though here not as wide as the total width of the threshold) and narrow between these points (plate II, fig. 9). The relation of this pad of tissue to the threshold as a whole is important and may best be understood by viewing a transverse section of the threshold (sagittal with reference to the trap as a whole). In such a section (fig. 5; plate II, figs. 3–5, 8) one sees the pad as a dense tissue forming the top of the threshold and bending over the outer margin. This bent-over part furnishes a surface for the free edge of the middle portion of the door to rest against when in a set position. As above stated, this margin is outwardly curved. To this curve fits the curve of the middle portion of the free edge of the door when in the set position. It may be observed that the raised outer marginal epithelium with its pad of glandular cells is supported by very large cells jutting upwards above the general level of their neighbors.

The pad ("Pflasterepithel" as Goebel called it) is of further and prime importance, in that *the cuticle of its glandular cells exfoliates* during development, and before the trap opens for business, *but remains attached by its forward margin.* This loosened cuticle thus forms a veil suspended between the horns of the threshold and attached to it along a line well below its forward margin at the forward limit of the pad. The presence of this veil has been hitherto overlooked; indeed, I have overlooked it myself for years. It is only with great care that sections can be cut (of fresh material, of course) without tearing it away. When it remains, it is so diaphanous that either it is not seen (in transverse sections of the threshold usually) or appears merely as the top of the threshold when seen looking along the sagittal axis. The forwardly directed surface of the pad and the veil form a pocket. It *thus comes to have a definite function as a valve, sealing the fissure between the edge of the door and the threshold,* just as a bit of leather stops the leakage of the piston head of a pump.

The exfoliation of the veil takes place rather late in the development of the trap. In bladders as small as 0.33 mm. in length it has not yet appeared but is recognizable at 0.47 mm. At these stages of development the door overhangs the threshold (GOEBEL) coming into its definitive position later. When first evident, it is to be observed over the outer one or two rows of pad cells, the exfoliation evidently beginning in this region and extending back (plate II, figs. 3–5, 8). In younger traps the veil appears more definite and circumscribed, but with age becomes more extensive and ill-defined at its loose posterior border. The ragged appearance of the loose margin of the veil is due to its irregular tearing away from the pad cells in the more interior region, that toward the inner margin of the threshold. The very thin ragged portion bears the evident imprint of the tops of the cells from which it arose.

A feature of the development of the veil must be especially mentioned, namely, that during the earlier period of its exfoliation there is an expansion of its area, so that it balloons away from the cells from which it arises. The impress of the cell top is, as a result, an exaggeration of the pattern present in a surface view of the pad. The large size of the meshes of the veil appears out of congruity with the smallness of the pad cells; it is only when the behavior during origin is known that the incongruity is removed.

The veil is cutinized (is insoluble in strong sulphuric acid) and yellows with iodine, when it can be easily seen. When bleached of iodine and lying in glycerin it becomes exceedingly diaphanous.

THE DOOR

The door, called by some the valve, is a structure of complex curvatures. It may best be described in relation to figures 1 and 3. Figure 3 is introduced for the further purpose of indicating my dissent from CZAJA'S mapping of the areas which he recognizes. His effort was concentrated on explaining the behavior of the door as a structure which presses down and outwardly on the threshold. Since this is not what happens, his description fails in cogency.

The insertion of the fixed margin of the door is along a U-shaped line, the plane of which is almost at right angles (*ca.* 100°) to the threshold plane, and so disposed that the free ends of the U coincide with the ends of the threshold where it gives on the side wall (fig. 1, *b c*). From this line of insertion the door hangs in such fashion that the free edge, that which articulates with the threshold, is nearly circular. This shape is retained normally by its own turgor. Plate II, fig. 6, is a photograph taken at right angles to the plane embracing the free edge of a freshly removed door. When in position, the thin edged sector (*a b c, a′b′c′*, fig. 3) is somewhat bent inwardly in adjusting itself to the threshold. In addition to this curvature, the door is also curved normally to the plane of the free edge. When forced by pressure into a nearly flat plane, it takes the form of fig. 7, plate II. There are, it is evident, as indicated in fig. 3, three regions—a middle generally circular area, truncated below to form the middle region of the free edge (*a a'*), and flanked by two triangular smaller pieces (*a b c, a'b'c'*) which fold along the lines *a c* and *a'c'* when the door is in position. The door is attached along *b c d c'b'*, the hinge at *d* being a strong curve which

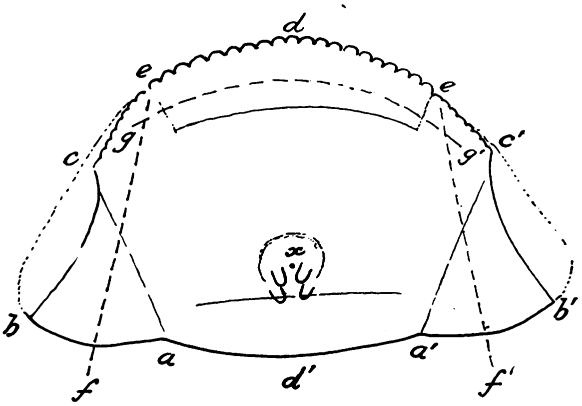

FIG. 3. Map of the door as seen when approximately flat.

b a a' b'. The free edge of the door.
a a'. Middle reach.
ab and a'b'. Lateral reaches.
ac and a'c'. Lines of the fold.
c a a' c'. Follow the curve of the threshold when the door is in the natural set position.
e f and e' f'. Approximate lines of lateral flexure.
g g'. Approximate line of transverse flexure. Median flexure occurs along the line d d'.
χ. Central hinge area; the base of the four trigger hairs are indicated, below which is the thickened margin or wale of the door.
b c and b' c'. Articulations of the door with the threshold.
c e and c' e'. Continuations of the lateral articulations against the wall of the trap.
e d e'. Transverse articulation.

is maintained in the transverse reach *g g'* to become in the lateral reach (*e c, e'c'*) a simple attachment. The structure of the wing *a b c* is continuous with that of the middle piece, and I am unable to identify the triangular areas plotted by CZAJA (*e f g* in his fig. 3, 1922, my fig. 3). The line of the bend, with which CZAJA seems to identify his triangle *e f g*, lies strictly along *a c, a'c'* in my fig. 3 (*e d* in his figure). When in position this line of bending follows the forward edge of the threshold from the horn (*c, c'*, fig. 4) to a point on this edge where the free edge of the door crosses (*a, a'*, figs. 1, 4) to the outer surface of the threshold. The chink formed between the fold of the door and the edge of the threshold lies behind the veil, which accordingly blocks it. CZAJA's account postulates a bend running above the thickened margin of the middle piece (*f f′ e′* in his figure), whereas as a matter of fact there is none there. He accords a corresponding discontinuity of structure indicated in his figure by lines. The fact seems rather to be that the structure of the lateral areas is completely congruous with that of the middle piece.

The narrow region below the insertion of the trigger hairs is much thickened and has a thick cuticle. The shape, as seen in section transverse to the run of the edge, is lenticular, the edge which rests on the outer surface of the threshold being rather sharp. Just at and above the insertion of the trigger hairs the door is very thin. This thin area is nearly circular and constitutes a hinge, allowing the thickened edge of the door to bend up and inwardly so that it can come just above the resisting edge of the threshold. When this condition is established, the door has little resistance and flaps inwardly, permitting an inrush of water. This concluded, it springs back into position, the stiff edge sliding over the pad till it regains its *ligne d'appui*. In doing so it pushes before it the loose veil which automatically comes into position as a valve not only near the horns of the crescentic threshold, as above stated, but along the whole length of the edge of the middle piece as well.

It is difficult, indeed, almost impossible to cut a section of fresh material so that the door remains in exactly the right position. A half-door inevitably curves free of the edge and lies more or less above the threshold, the veil then looking like a ragged mass of stuff not calculated to attract attention. I have accordingly studied the silhouettes of entire fresh traps making negatives with long exposures. These, when examined, usually show a shadow made by the veil, and the door in its proper position. Once one knows what to look for, it is quite possible, often easy, to see the veil in the living trap by looking obliquely into the entrance with a low power objective. In some cases even the quasi-cellular structure can be seen (plate II, figs. 1, 2, 10).

Little has been said yet about the hinge of the door as a whole. In the transverse reach this hinge is a strong flexure toward the inside of the trap, bending back again into the curvature of the middle piece. As the transverse reach fades into the lateral reaches, the bend of the hinge becomes less pronounced, until it merely curves downwards and a little away from the wall. In the region over the end of the threshold a mass of tissue lifts the end of the door (marked *b c, b′ c′*, fig. 1) away somewhat from the wall, a group of large cells, a sort of buttress, causing this (*c, c′*, fig. 1, 4). This grades in the forward direction into the wall and offers attachment to the stretch of the arch *b* to *e*, fig. 1. At point *e* there occurs a slight angle, breaking a little the continuity of the arch, the point at which the strongly bent hinge cells (*e d e′*) begin.

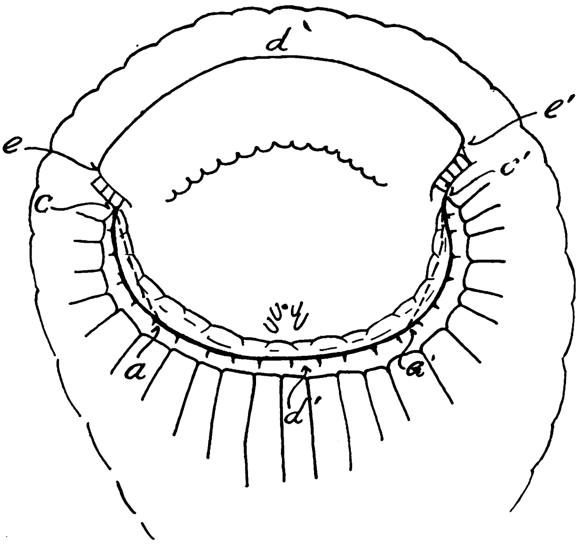

FIG. 4. Diagram of the entrance from the inside of the trap.

The behavior of these regions of the door along the arch of attachment may be seen by studying the silhouette of a trap which has swallowed a glass rod (fig. 2). A trap freed from the plant will, when the end of the glass rod is pushed against the trigger hairs, jump forward and swallow the end of the rod, as CZAJA found using a needle. I found that a rod 0.1 mm. in diameter is easily swallowed. If the rod is tapering, it may be pushed forward, with precautions to do no damage to the entrance mechanism of the trap, till the door is opened to its maximum. When in this position the rod was 0.17 mm. in diameter, representing approximately the maximum possible displacement of the door, probably more than normally occurs. The middle piece of the door (*f*, *e*, *e′ f′*, fig. 3) suffers maximum displacement, the sides of the door being bent upwards approximately along the lines *e f* and *e′f′*, fig. 3. This bend is most pronounced toward *f*, and towards *e* gradually fades into the curvature between *e* and *e′*, though not without a jog at these points. The tissues along $e-f$ and $e'f'$ are thus strongly pulled out of equilibrium and tend to straighten back in a direction normal to $e-f$ and $e-f'$. The cells at right angles to the line $g-g'$ tend to bend back normally to this line. It is certain that the cells along *b c e* and *b′c′e′* are displaced from position only very slightly, merely enough to accommodate themselves to the sharp upward bend along *e f* and *e′f′*.

What the maximum displacement of the door is when it opens by displacement by the water column pressing against it cannot precisely be said, but, since (in the trap I measured) the maximum opening has the transverse diameter of 0.17 mm. and the same trap immediately, on springing the door, swallowed a rod 0.1 mm. in diameter, it must open more widely than has been supposed. MERL speaks of a lunate "halbmondförmig" slit. Any opening short of a good-sized throat could not engulf the large objects often found in the traps; and it must not be forgotten that during the time the door is open, less than 1/16 of a second, a column of water fully 1 mm. long passes in. During the movement of this column the door must remain stationary in a position presenting a throat of diameter greater than 0.1 mm. To do this the sides of the door must be bent upwards, approximately, though not as much, as in fig. 7.

The recovery of the set position of the door does not wait on the complete relaxation of the lateral walls, and in fact probably always closes before. This is shown by the fact that, after any event of tripping, the walls will on puncturing the bladder with a sharp needle relax further to the maximum possible extent (**12**). The fact is used here to emphasize the vigorous action of the door, which recovers its position in spite of a still inflowing column of water. The change in shape of the trap after tripping with a needle and after puncturing with a needle was illustrated by MERL.

Flexure of the door also occurs along the line *d d′* in the sense opposite to the flexure *e f* and *e′f′*. The great thickness and elasticity of the door

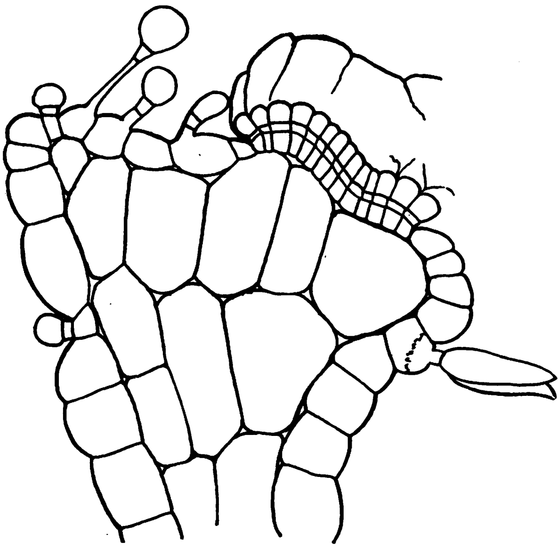

FIG. 5. Transverse section of the threshold showing the veil when fully developed.

edge, forming a wale of tissue reaching from a to a', enable it, while bending before the moving column of water, on release of pressure to immediately resume its semicircular form, bringing it back into its original position, the whole edge from b to b' (fig. 3) being in the form of an unbroken arch (plate II, fig. 6). This wale of tissue is important, therefore, in bringing the door into the set position. Its initial flexure, due to the leverage by the trigger hairs, is at its middle point (d'). The pressure of the water causes it to arch in the opposite sense, the flexure spreading outwardly along the radii from the centre x.

Correlated with the remarkable degree of flexure possible, and with the strong resistance of the door to deformation, is the form of the cell walls. These are never straight, but curved like so many springs. This is true of both radial and periclinal walls (plate II, fig. 7). This is, of course, a matter of common observation. What is important for the correct understanding of the working of the door is the proper evaluation of the rôle of the thickened wale along the middle reach of the door edge. This acts by swinging into position, engaging the outer edge of the threshold as a catch which in spite of its firm engagement can be easily released by downward pressure of the trigger hairs. Its almost cartilaginous consistency is due in large part to the much thickened outer walls (MERL) of the very small cells.

Summary

It has been shown in the foregoing that when the trap of *Utricularia minor* is in the set position, the middle part of the free edge of the door rests against the outer surface of the pad of glandular cells of the threshold, and not, as heretofore supposed, against the top or any part of the top or against the edge of the pad. It maintains its position against water pressure by virtue of the resistance offered by the threshold. The outer reaches of the door edge cross obliquely the sides of the threshold. There is of mechanical necessity, therefore, a fold between the middle and lateral portions of the door which would, if not otherwise provided against, allow inflow of water under the reduced pressure known to be present in the trap when set. This possible leakage of water into the interior of the trap is prevented by the presence of a veil or curtain attached to the outer surface of the threshold and stretching from one horn to the other of the crescentic threshold in such a manner as to act as a valve to exclude water by pressing on the edge and folds of the door. This veil, or valve, is the outer cuticle released from the cells of the pad, being set free from the inner margin of the pad and remaining firmly attached in front. The veil shows the imprint of the top of the cells from which it sprung. The earlier formed part of the veil suffers considerable extension, or ballooning, recalling the behavior of the cuticle in certain other glandular trichomes (*Pelargonium*). The veil arises during the later period of development of the trap, so that when the trap begins to function as such, the veil is ready in position.

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EXPLANATION OF PLATE

FIG. 1. Entrance of trap viewed from the outside showing the veil and the upper surface of the threshold. The door is sprung outwardly by its own turgor, but it is so seen because a part of it has been removed in sectioning the trap.

FIG. 2. The veil and front edge of the threshold of another trap. The lower edge of the door can be seen again in the sprung position.

FIG. 3. Section of the threshold of a young trap showing the exfoliating cuticle at a rather early stage.

FIG. 4. A somewhat later condition.

FIGS. 5 and 8. The fully developed veil as seen in transverse section of the threshold.

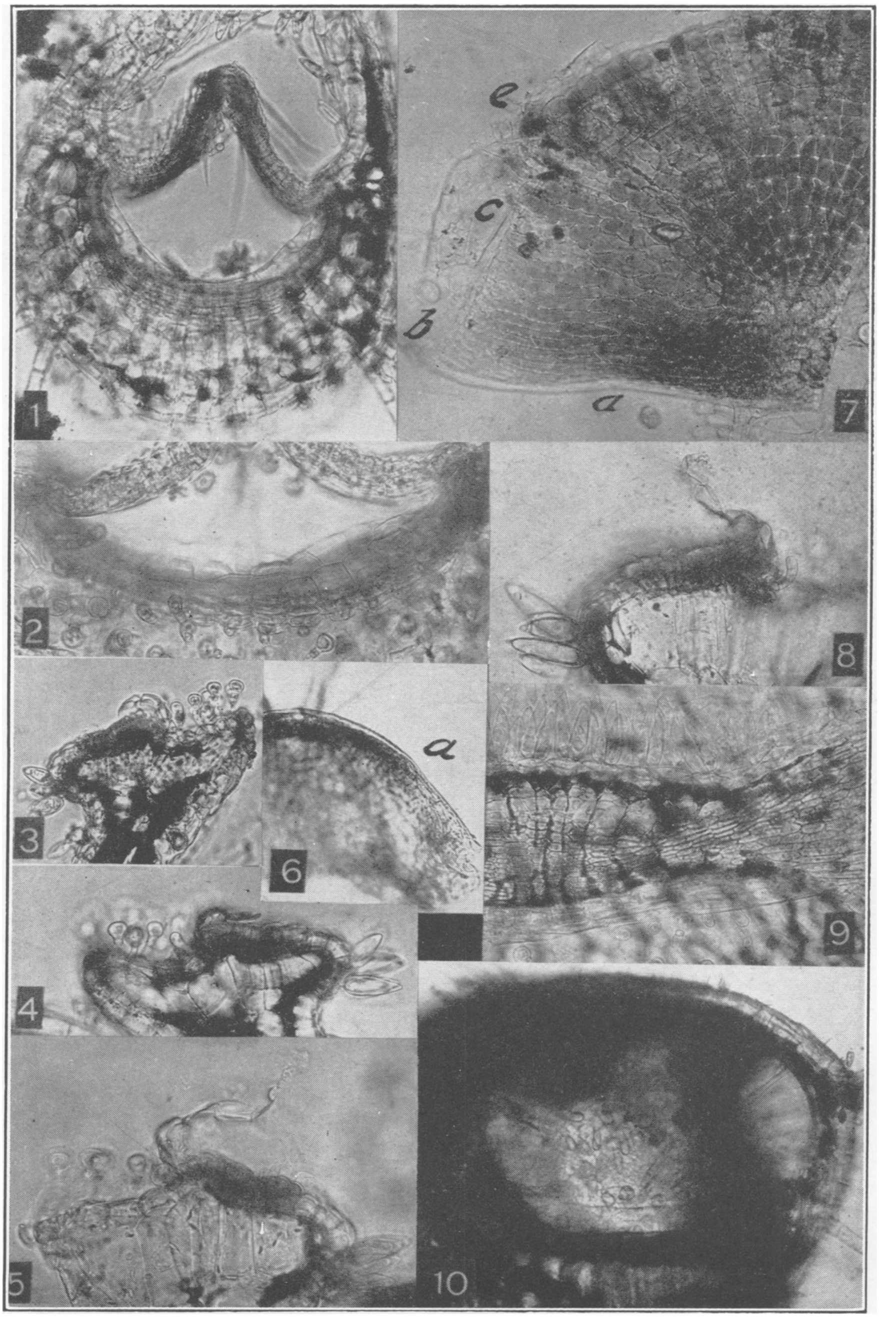
FIG. 6. Half of the door showing the thick wale above the middle reach of the lower edge and the thin lateral portion which crosses the threshold from *a* to *b*—text fig. 1.

FIG. 7. A half-door laid out nearly flat viewing the inside surface. Letters as in text fig. 1.

FIG. 9. View of a little over half a threshold seen from above. The anterior margin bears the veil. The inside face of the threshold (above) bears glandular trichomes. The trapezoidal cells of the pad can be seen. The dark patches are caused by air in the intercellular spaces, here as in other figures.

FIG. 10. View of the door and veil in the set position as seen when looking into the threshold of a living set trap.

1022



LLOYD–UTRICULARIA